

Research Article

Relative importance of propagule size and propagule number for establishment of non-indigenous species: a stochastic simulation study

David Drolet^{1,2*} and Andrea Locke³¹*Department of Health Management, Atlantic Veterinary College, University of Prince Edward Island, 550 University Avenue, Charlottetown, Prince Edward Island, C1A 4P3 Canada*²*Current address: Fisheries and Oceans Canada, Institut Maurice-Lamontagne, 850 route de la Mer, Mont-Joli, Québec, G5H 3Z4 Canada*³*Department of Fisheries and Oceans Canada, Gulf Fisheries Centre, P.O. Box 5030, Moncton, New Brunswick, E1C 9B6 Canada*E-mail: david.drolet@dfo-mpo.gc.ca (DD), andrea.locke@dfo-mpo.gc.ca (AL)

*Corresponding author

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Abstract

Propagule pressure is emerging as the most consistent predictor of establishment in non-indigenous species. Increasing propagule size (the number of individuals arriving in a novel environment at one time) is thought to increase probability of establishment by counteracting demographic stochasticity and Allee effects. Increasing propagule number (the number of introduction events) is thought to increase probability of establishment by counteracting environmental stochasticity. However, the relative importance of these effects and the conditions under which one effect may become predominant is largely unexplored. We first used stochastic population simulations, with a constant number of immigrants distributed over varying numbers of introduction events, to determine the relative importance of propagule size and number on the probability of establishment. Simulations were conducted under different environmental stochasticity and Allee effects regimes with parameters set to be representative of species with high risk of invasion. In absence of Allee effects, there was a slight increase in probability of establishment when going from very low to low propagule number. However, when Allee effects were included, probability of establishment consistently decreased with increasing propagule number. This pattern was consistent across a wide range of parameter values, and tended to be more pronounced when other model parameters resulted in low probability of establishment. This suggests that, within a range of conditions representative of non-indigenous species at high risk of invasion, large infrequent introductions are riskier than smaller more frequent ones. This is particularly true when Allee effects are likely to influence population dynamics at the early stages of the invasion process.

Key words: propagule pressure, invasive species, colonization, stochastic population models, Allee effects

Introduction

A major goal of invasion biology is to predict establishment and spread of a newcomer following its arrival in a novel environment. Initially, research focused on identifying the species-level traits of successful invaders (e.g., Rejmanek and Richardson 1996) and the characteristics making a community prone to invasions (e.g., Levine et al. 2004). However, it is becoming increasingly clear that propagule pressure (the total number of individuals introduced to a novel environment within a given time interval) is the most consistent predictor of establishment (Lockwood et al. 2005; Simberloff 2009). Larger numbers of immigrants increase the probability that an introduced

population will persist (e.g., Cassey et al. 2004; Memmott et al. 2005; Korsu and Huusko 2009; Blackburn et al. 2013; Britton and Gozlan 2013). In addition, propagule pressure may confound species traits (Simberloff 2009; Colautti et al. 2006), overwhelm community characteristics (Von Holle and Simberloff 2005), and overcome unfavourable abiotic conditions (Warren et al. 2012) in explaining establishment.

Propagule pressure can be decomposed into two parts: propagule size (the number of individuals arriving during an introduction event) and propagule number (the number of introduction events) (Simberloff 2009). These two components are thought to influence probability of establishment through different mechanisms. Propagule

size can influence the severity of Allee effects: a positive density-dependence in population growth rates (Courchamp et al. 1999). Allee effects were detected in experimental introductions (Grevstad 1999a; Fauvergue and Hopper 2009) and theoretically shown to reduce probability of establishment (Grevstad 1999b; Drake and Lodge 2006), i.e., introductions based on small propagule size were more likely to fail when Allee effects were present. Propagule size is also thought to affect the influence of demographic stochasticity. Small propagule sizes are more likely to fail in establishing populations because random variation in reproduction and survival induces relatively more pronounced fluctuations in small than large populations (Lande 1993; Simberloff 2009). Conversely, propagule number is expected to decrease the effect of environmental stochasticity; more frequent introductions temporally spread the risk and make it less likely that short-term occurrence of poor conditions will eliminate all immigrants arriving over the time period (Grevstad 1999b; Simberloff 2009).

Three empirical studies have attempted to evaluate the relative importance of propagule size and number on the probability of population establishment, and none have addressed the influence of Allee effects. Drake and Lodge (2005) varied propagule size and number in laboratory populations of the parthenogenetic freshwater zooplankter *Daphnia magna* Straus, 1820. They found that population size at the end of the experiment was positively influenced by propagule number, with more frequent introductions resulting in larger populations. However, *D. magna* being parthenogenetic eliminates the potential role of reproductive Allee effects. Hedge et al. (2012) varied propagule size and number (keeping the total number of individuals constant) using larvae of the oyster *Crassostrea gigas* (Thunberg, 1793) in a field experiment. They found that settlement was higher with more frequent smaller introductions, which was attributed to the effect of environmental stochasticity and/or facilitation among settlers of different ages. However, the experiment terminated while the populations were still only composed of juveniles, making potential reproductive Allee effects undetectable. Finally, Britton and Gozlan (2013) manipulated propagule size and number (keeping the total number of individuals constant) using the invasive fish *Pseudorasbora parva* (Temminck and Schlegels, 1846) in experimental ponds over a period of three years. This design would allow detection of Allee effects, but all replicates established a population. Therefore, the relative importance of

propagule size and number for the probability of establishment of sexually reproducing species, where Allee effects are likely, is still unknown from empirical studies.

Stochastic population models have been used widely in conservation biology. For example, they can be used to evaluate the probability that an endangered population will persist over a certain time span (population viability analyses; Akçakaya and Sjögren-Gulve 2000) and the smallest population size that keeps the probability of extinction below a specified level (minimum viable population; Traill et al. 2007). Establishment, the reverse of extinction, can be used to investigate colonization processes (e.g., Drake and Lodge 2006). Such models have been used by Grevstad (1999b) to inform best release strategies for biocontrol agents when a fixed number of individuals is available. She found that, at high levels of environmental stochasticity, the probability that at least one population persisted was greater if fewer individuals were released at multiple independent sites. Conversely, in the presence of Allee effects, larger introductions at fewer independent sites were more effective. In presence of both, an optimal release strategy could be determined, depending on the severity of both Allee effects and environmental stochasticity. In a similar study, Wittmann et al. (2014) investigated time taken by a population to reach a certain size under various scenarios of propagule size and number, while keeping propagule pressure constant. They found that, in easy conditions (i.e. positive population growth rate at all population sizes) populations grew faster with smaller, frequent introductions, whereas the converse was true in difficult conditions (i.e. negative population growth rate at some population sizes).

Here we developed stochastic population models to investigate the relative importance of propagule size and number on the probability of establishment in a situation where introductions are non-independent, i.e. immigrants influence local population dynamics. This was first done under different regimes of environmental stochasticity and Allee effects, with parameters chosen to be representative of species posing a high invasion risk. We then conducted a sensitivity analysis to evaluate the consistency of the patterns when a much wider range of conditions is modeled. Our study should be helpful from a management perspective as it allows understanding the vectors of introduction more likely to result in invasions. These vectors can then be prioritized for management interventions.

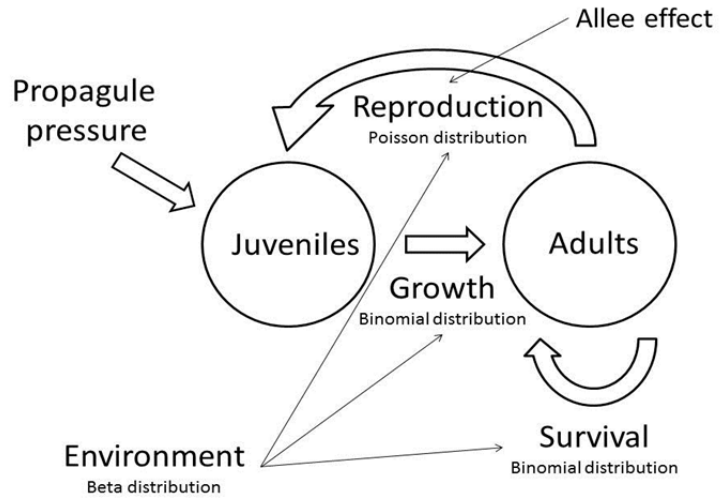


Figure 1. Schematic representation of the stochastic model used to investigate the relative influence of propagule size and number on the probability of establishment of non-indigenous species.

Methods

We developed simple stage-based, discrete-time, stochastic population simulations with compartments for abundance of juveniles and adults (Figure 1). Change in abundance of juveniles is a function of propagule pressure (in this model, all immigrants are juveniles) and abundance of adults (adding to the juvenile population through reproduction). Per capita rate of reproduction is influenced by abundance of adults through the Allee effect. Change in abundance of adults is a function of abundance of juveniles (through growth), and abundance of adults (through survival) (Figure 1). All vital rates (growth, survival and reproduction) are influenced by environmental stochasticity. We thus have a system of two equations:

$$J_{t+1} = \text{Beta}(\alpha, \beta)_t \frac{\sum_1^{A_t} \text{Poisson}(\lambda)}{1 + \left(\frac{A_t}{X_0}\right)^{-b}} + I_t$$

$$A_{t+1} = \text{Beta}(\alpha, \beta)_t \left(\text{Binomial}(A_t, p_a) + \text{Binomial}(J_t, p_j) \right)$$

where J_t is abundance of juveniles in the population at time t , $\text{Beta}(\alpha, \beta)_t$ is time-specific environmental stochasticity coming from a beta distribution with shape parameters α and β , A_t is abundance of adults at time t , λ is the mean per capita fecundity coming from a Poisson distribution, X_0 and b are parameters that determine the shape of the sigmoidal reproductive Allee effect, I_t is

the number of individuals (propagule size) arriving at time interval t , $\text{Binomial}(A_t, p_a)$ and $\text{Binomial}(J_t, p_j)$ represent survival of adults and growth of juveniles, coming from binomial distributions with a number of events equal to population size and probabilities of p_a and p_j . In the simulations, introduction of individuals occurred after growth, survival, and reproduction (which occurred simultaneously).

Environmental stochasticity was modeled with a beta distribution without temporal autocorrelation among time intervals (i.e., value at time $t+1$ is independent of that at time t). The shape parameters were selected to obtain a majority of time intervals where vital rates were close to their maximum, and a low proportion of time intervals where rates were greatly reduced ('J-shaped' distributions; Figure 2A). The mean was set to 0.95 and the α - and β -parameters were manipulated to change the variance, with increasing variance corresponding to more severe stochasticity. Note that these simulations were also run using unimodal symmetrical beta distributions (time intervals with rates at an intermediate level of their maximum with variation around the mean); the results were very similar and are thus not presented here.

The probability of growth of juveniles (p_j) and survival of adults (p_a) were set to 0.1 and 0.5, respectively, and the mean number of offspring per capita (λ) was set to 8. In the absence of Allee effects, this resulted in a positive average population growth rate of 1.12. At high population sizes, the calculations for the binomial and Poisson distributions were computationally heavy.

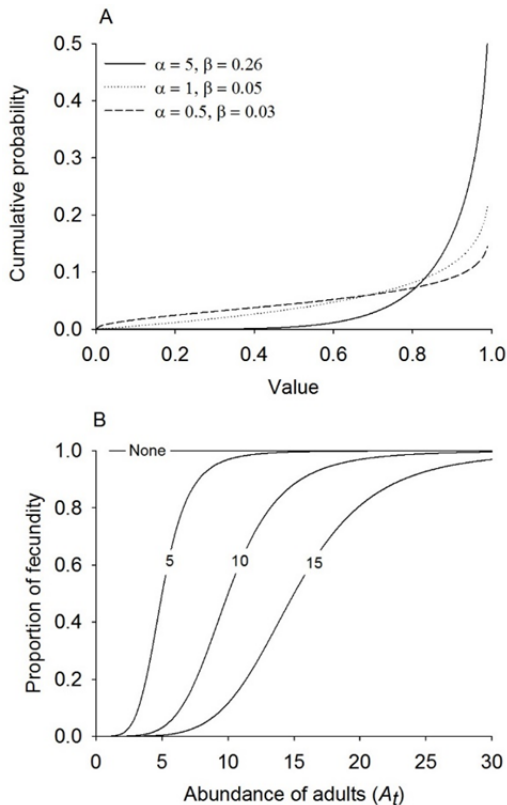


Figure 2. Visual presentation of parameters used in the simulations. A) Cumulative probability distributions for the beta distributions (and associated parameters) used to simulate environmental stochasticity. B) Proportion of maximum fecundity as a function of abundance of adults used to simulate Allee effects of different severity. Numbers on the lines show the X_0 parameter that modifies the number of adults required for Allee effects to dampen. “None” indicates the case with no Allee effect.

Therefore, if the abundance of a stage (juveniles and adults) exceeded 1000 individuals the raw probability or number was used (if $J_t > 1000$ survival of juveniles was set at 0.1, and if $A_t > 1000$ survival of adults was set at 0.5 and per capita reproduction was set at 8), and the vital rates were solely influenced by environmental stochasticity. These abundance thresholds were well above the values where demographic stochasticity played an important role in the simulations.

To model reproductive Allee effects, we adjusted per capita reproductive output using a sigmoid function of abundance of adults. The shape parameter b (setting the steepness of the increase) was set to 5, and we varied X_0 which determines how many adults are needed for the Allee effect to dampen. We ran simulations in the absence of Allee effects and with values of X_0 of 5, 10, and 15 (Figure 2B).

We varied propagule size and number while keeping the total number of individuals at 1000, going from one introduction event of 1000 individuals to 50 introductions of 20 individuals (by increments of one introduction). The first introduction event always occurred during the first time interval, and the remainder were randomly distributed among the following 49 time intervals. Note that we also ran simulations with the certain introduction occurring at time 25; the results were very similar and are not presented here.

Each combination of propagule size and number, Allee effect, and environmental stochasticity was simulated 1000 times, in ten groups of 100. The simulations ran over 100 time intervals, i.e., the 50 intervals when introductions do or can occur and an extra 50 intervals when no more introductions occur. At the end of each time interval, the number of juveniles and adults were rounded to the nearest integer so that discrete distributions (binomial and Poisson) could be generated. For each group of 100 simulations, we noted the probability of establishment, i.e., the proportion of simulations for which the final number of individuals was above 0 at time 100. To smooth patterns, we then calculated the mean for the 10 groups for each scenario simulated.

Model structure and parameters in this first set of simulations were selected to be representative of the establishment process of high-risk invasive species. For this reason, we did not consider negative density-dependence in the simulations. If a species is to become invasive, it will by definition eventually become very abundant, but carrying capacity is not likely to be reached rapidly. Going into an exponential growth phase is the most likely scenario for the early stages of a successful invasion, and we expect that negative density-dependence will only come into play well after the population has reached invasive proportions. Also, the highest level of environmental stochasticity used in the initial simulations was at the limit of what would be expected for high-risk invaders; higher variance resulted in population sizes that oscillated widely, and some went extinct after the introductions had stopped (i.e., between time intervals 50 and 100). This would correspond to a situation where the environmental tolerance of the species is exceeded by the level of environmental variation, and consequently such species would not, in these instances, be considered a problem in the receiving area.

We further investigated the generality of patterns at higher levels of environmental stochasticity.

A second set of simulations was conducted (as above) but in the absence of Allee effects and with the α parameter of the beta distribution for environmental stochasticity set at 0.5, 0.2, 0.05, and 0.01.

We conducted a sensitivity analysis, following the general methodology of McCarthy et al (1995), to determine if patterns of establishment are consistent when a wider range of conditions (than those selected in the initial simulations) is considered. We ran a third set of simulations, with a unique set of conditions for each iteration, in which model parameters were randomly drawn from uniform distributions. The probabilities of survival for juveniles and adults (p_j and p_a) ranged from 0.01 to 1, average per capita number of offspring (λ) ranged from 1 to 20, the shape parameter for Allee effects (X_0) ranged from 0 to 50, and the shape parameter of the beta distribution for environmental stochasticity (α) ranged from 0.1 to 5. The β parameter was manipulated to keep the mean at 0.95; this resulted in variances ranging from 0.009 to 0.045. We also varied total number of individuals introduced in the system using a discrete uniform distribution ranging from 100 to 2500. Propagule number was again between 1 and 50 with values coming from a discrete uniform distribution; the number of individuals per introduction event was total number of individuals divided by propagule number, rounded to the nearest integer. A total of 50000 population trajectories were simulated and we kept track of whether each resulted in establishment or extinction. We then fitted a generalized additive model (GAM) with the loess smoothing algorithm, using the different parameters as continuous independent variables and establishment as the dependent variable (binary response, 0 = non-establishment and 1 = establishment; the logit link function was used). Residual inspections showed the GAM provided a good fit to the data and was superior to a similar generalized linear model as many effects were non-linear.

The overall effect of propagule number in the sensitivity analysis was isolated by plotting probability of establishment predicted by the GAM for each simulation against the number of introductions selected for this particular simulation. Given the high number of data points, we averaged predicted values for the different propagule numbers (by increments of 2) for ease of visual interpretation. We used a similar procedure to evaluate how propagule number interacted with the other parameter in the model. We produced mesh plots of averaged predicted values over the

range of the variables considered (increments were set to obtain a five by five grid). Given the results obtained in the first and second sets of simulations and the coarse plotting technique used, we decided to run a second sensitivity analysis focussing on cases with no Allee effect, high environmental stochasticity, and low propagule numbers. The same methods were used, but the range of the α parameter was restricted from 0.1 to 1, while the number of propagule ranged from 1 to 15.

Results

In the initial simulations, trends in total population size over time fell into four qualitative groups. In the first group, the population went into exponential growth phase immediately (Figure 3A). In the second, a few or several propagules failed to establish; the population went extinct several times before going into exponential growth phase (Figure 3B). Third, all propagules failed and the population never established (Figure 3C). Fourth, the population initially established but never went into exponential growth phase; these resulted in either extinction by the end of the 100 time intervals or establishment but at low population size (Figure 3D).

Not surprisingly, increasing Allee effects and environmental stochasticity had a negative influence on the probability of establishment. The effect of propagule number on the probability of establishment interacted with both Allee effects and environmental stochasticity. At low environmental stochasticity, and no or mild Allee effect, all simulations resulted in establishment. With increasing severity of Allee effects, large infrequent propagules resulted in 100% establishment, followed by a monotonic decrease in probability of establishment with increasing propagule number (Figure 4A). In other words, many small introductions resulted in a lower probability of establishment than a few large introductions under these conditions. At a moderate level of environmental stochasticity, overall probability of establishment decreased; not all populations established at no to mild Allee effects. In addition, there was a slight increase in probability of establishment when going from 1 to ~5 propagules at all Allee effects (Figure 4B). At high environmental stochasticity, probability of establishment initially increased with increasing propagule number, but either levelled (no or mild Allee effects) or decreased (moderate or strong Allee effect) when propagule number was greater than ~5 (Figure 4C). Increasing variance of

Figure 3. Examples of population trajectories for the four qualitative outcomes. A) population went into exponential growth after the first introduction, B) a few initial propagules failed to establish, but population eventually went into exponential growth, C) all propagules failed and population did not establish, and D) population never went into exponential growth; it either persisted at low numbers or went extinct between time intervals 50 and 100.

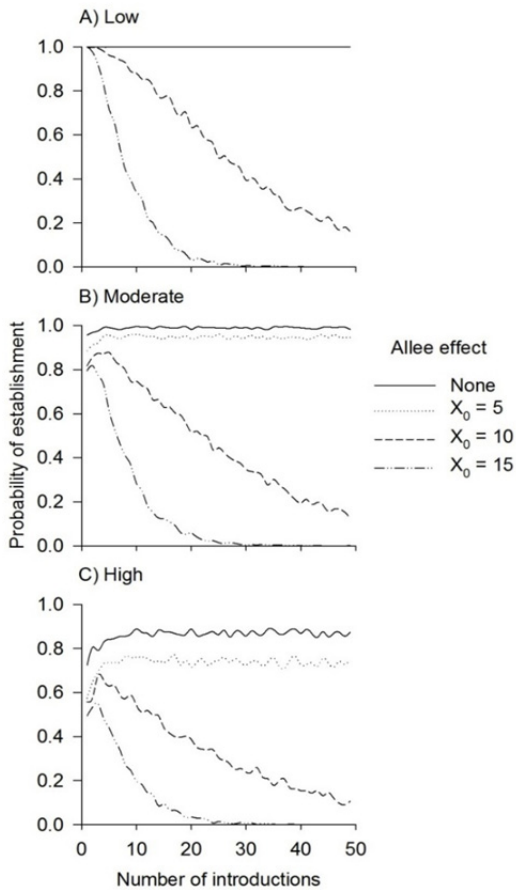
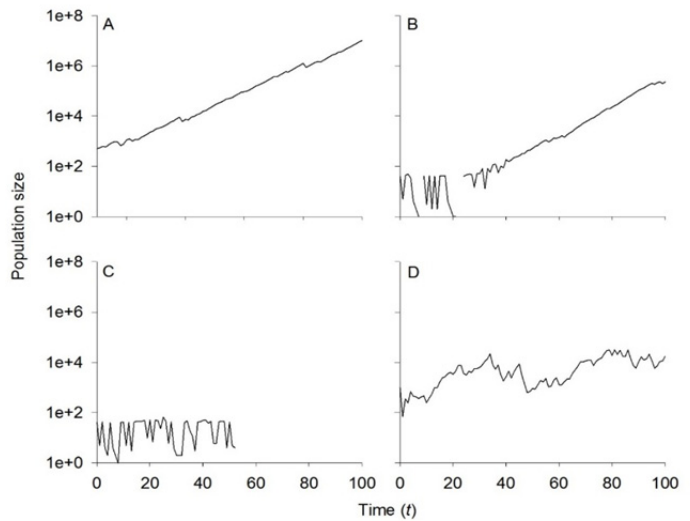


Figure 4. Probability of establishment in relation to number of propagules; the total number of individuals introduced was kept constant. Panels show the results for A) Low, B) Moderate, and C) High levels of environmental stochasticity. Lines show the results under Allee effects of different severity.

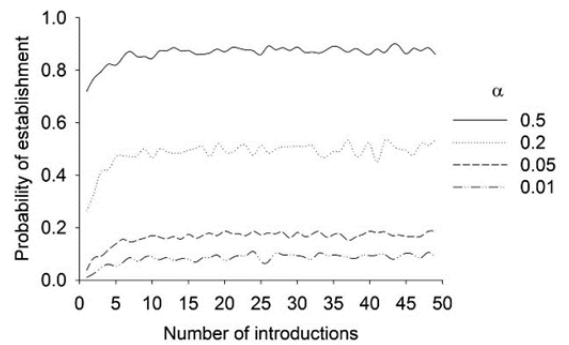


Figure 5. Probability of establishment in relation to number of propagules at high levels of environmental stochasticity; the total number of individuals introduced was kept constant.

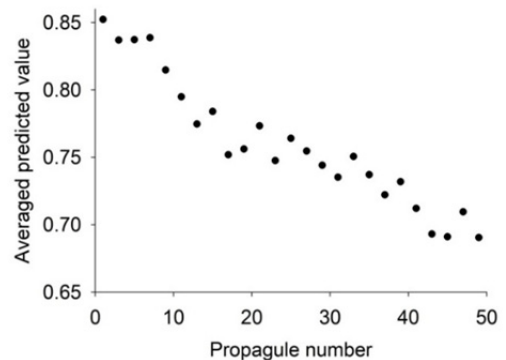


Figure 6. Overall influence of propagule number on probability of establishment of non-indigenous species from a sensitivity analysis. Values are averaged probability of establishment predicted by a Generalized Additive Model over the range of propagule number.

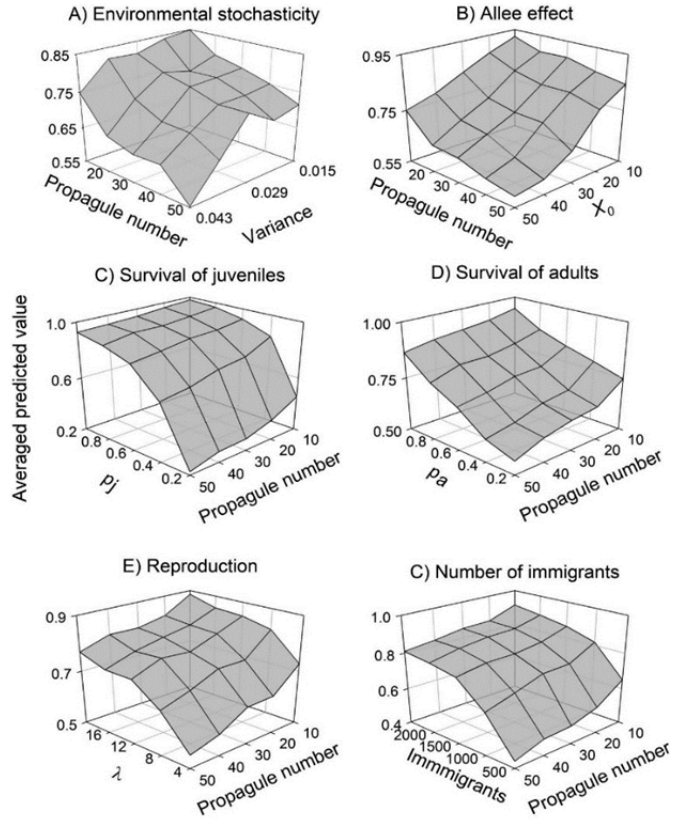


Figure 7. Interaction between propagule number and other model parameters on probability of establishment of non-indigenous species. Values are averaged probability of establishment predicted by a Generalized Additive Model over the range of value considered for each variable.

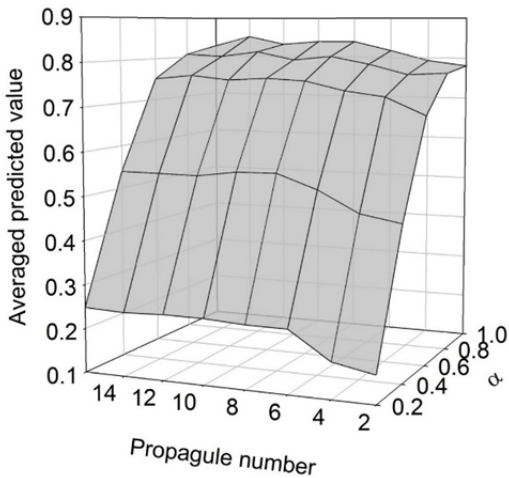


Figure 8. Interaction between propagule number and environmental stochasticity. Values are averaged probability of establishment predicted by a Generalized Additive Model, on population simulations not including Allee effects, over the range of values considered for each variable.

environmental stochasticity beyond the range initially considered (in absence of Allee effects) resulted in similar patterns: an initial increase in probability of establishment at low propagule number, followed by a plateau at higher propagule numbers (Figure 5).

The results of the sensitivity analysis further confirmed the importance of propagule number on the probability of establishment. When the variability related to all other factors was taken into account, averaged probability of establishment decreased with increasing propagule number (Figure 6). On average, scenarios where one or two large introductions occurred had a higher probability of establishment by $\sim 0.15\text{--}0.20$ when compared to very frequent smaller introductions. The effect of propagule number on the probability of establishment interacted with all the other variables included in the GAM (Figure 7A–F). In general, propagule number had a greater influence when the other variable was towards the end of the spectrum leading to lower probability of establishment; in other words, propagule number was more important at low probability of establishment. For example, propagule number had a very

small influence when survival of individuals was high, but induced a relatively greater change when survival was low (Figure 6C–D). Finally, when no Allee effect was included in the population simulations, there was a slight increase in probability of establishment when propagule number increased from ~ 1 to 5, and did not vary at higher propagule number (Figure 8).

Discussion

It is generally accepted that larger introductions dampen the effects of 1) demographic stochasticity and 2) Allee effects, whereas 3) frequent introductions dampen the effect of environmental stochasticity (Simberloff 2009). However, there are still unanswered questions about the relative importance of these effects and the conditions under which one may become predominant. Within the range of parameters used (in particular the number of immigrants; see also Grevstad et al 2011), we found no support for the first conclusion, similar to Grevstad (1999b). Had demographic stochasticity played an important role, we would have expected a decline in probability of establishment with increasing number of propagules when Allee effects were absent. In addition, there was no negative link between probability of establishment and propagule number, even at low number of immigrants in the sensitivity analysis (data not shown). Our results are consistent with the second conclusion; when moderate/high Allee effects were simulated, frequent small introductions consistently resulted in lower probability of establishment than fewer larger introductions. This is similar to Grevstad (1999b) who found a higher probability of at least one population establishing with a few large independent introductions (i.e. simultaneous introductions at different sites) when compared to numerous smaller introductions. In our model, the introductions are non-independent; migrants can interact with individuals already present. Therefore, there is a possibility that frequent arrival of individuals could keep the population above the threshold where Allee effects are no longer important. We found no evidence for this compensation; even Allee effects of the mildest intensity were not dampened by nearly constant arrival of individuals. Note that this result could change if adults were introduced (instead of or in addition to juveniles) since Allee effects influence only reproducing adults and there is a delay between arrival of juveniles and their maturation.

It is important to note that inclusion of Allee effects in the simulation is the sole reason for the negative link between probability of establishment and propagule number. In absence of Allee effect, there was a positive relationship between probability of establishment and number of propagules, which is partially consistent with the third conclusion. This positive link was only observed at very low number of propagules (between one and \sim five) and the increases were small when compared to the declines induced by Allee effects. Much more pronounced increases were observed by Grevstad (1999b) in particular in the absence of Allee effects, and she did not observe a plateau at a higher number of propagule (comparing Figure 5 with Figure 4B in Grevstad [1999b]). This might be the result of differences in modeling environmental stochasticity; we could not backtrack the mean of the beta distribution used by Grevstad (1999b). This may also be the result of differences in questions asked; she was interested in probability that one of the independent introductions established whereas we were interested in probability of establishment of one population submitted to non-independent introductions. Despite some differences, our results are in line with those for independent introductions.

It is interesting to note that propagule number was more important when other variables were towards the end of the spectrum leading to lower probability of establishment. This appears to be in accordance with the results of Wittmann et al (2014). They found that simulated populations grew the fastest with large, infrequent introduction in difficult conditions (i.e. negative population growth rates); this would be analogous to our situations with, for example, low survival or reproduction rates. However, in easy conditions (positive population growth rate), they found the fastest growth rates with small, frequent introductions. In our model, we did not see this reversal in trend (except for a small increase in probability of establishment when going from 1 to \sim 5 propagules, followed by a plateau), but propagule number was much less influential when other variables were more benign. This difference could be the result of variation in model structure between the two studies. Wittmann et al. (2014) analysed time take by the model populations to reach a certain size; it is possible that multiple smaller introductions result in a population that starts growing sooner and therefore reach the target size faster. Similar modeling results were also obtained by Rajakaruna et al. (2013) who found

an increase in probability of establishment within increasing immigration stochasticity (equivalent to situations with large infrequent introductions) in unfavorable conditions, while the reverse was true in favorable conditions.

Our results could also bring insights into reintroduction programs for endangered species. However, caution must be taken as our model is representative of endangered species, if, and only if, the number of individuals released is much smaller than the carrying capacity of the release area (see Drake and Lodge [2006] for a demonstration of the importance of carrying capacity in influencing the effect of propagule pressure). If managers have concerns about the quality of the environment, i.e., the resources are not sufficient to sustain a large number of individuals (which is likely for species extirpated by habitat degradation) then a model including a term for carrying capacity would be more suited. This could considerably change the patterns in establishment related to propagule number. However, the general approach could be adapted to determine whether, and under which conditions, a large simultaneous release is a better reintroduction strategy than several smaller releases.

We conclude that, within a range of parameters relevant to non-indigenous sexually reproducing animals with simple two-stage life cycles and with a high risk of invasion, Allee effects have a high influence on the probability of establishment. As such, few large introductions are riskier than more frequent smaller ones. Our model therefore suggests that managers trying to prevent establishment of a species likely to become invasive in an area should target rare vectors likely to carry a large number of immigrants, as opposed to more frequent vectors carrying fewer individuals. This recommendation should be taken cautiously as it will be very difficult to determine *a priori* the total number of individuals being transported. However, there may be applications for management of vectors such as ballast water or hull fouling, where decisions may need to be made on the relative risks of different classes of shipping so as to prioritize transportation pathways or vessel types for regulation or research (e.g., DFO 2014). Our simulations used a simple life cycle that is consistent with many taxa but may not be representative of some animals, plants or algae that have more complex life history strategies. Future work could use more complex models to evaluate how, for example, delayed maturity, or dormancy, influences the generality of our results.

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